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## THE CHROMOSOME COMPLEX OF ORTHOPTERAN SPERMATOCYTES.

C. E. McCLUNG.<sup>1</sup>

A subject of perennial interest is offered by the maturing germ cells, and that appreciation is not lacking is well evidenced by the large annual output of papers devoted to different phases of the question. The task of keeping abreast of this literature has become a considerable one, especially since it is now necessary to take into account the investigations upon hybrid matings and upon unusual or modified methods of fertilization. Despite regret at the increased labor thus brought about, one cannot but rejoice at the enlarged conceptions of chromosome functions which have followed from this union of two apparently different lines of investigation.

It cannot be gainsaid, I think, that as our knowledge increases it becomes more and more evident that in the chromosomes we are dealing with intracellular elements of definite morphological character which are self-perpetuating and which have to do with the development of precise characters in the organism of which they are a part. In my early study of the male germ cells of insects I became convinced of this individuality of the chromosomes, and in all my papers I have emphasized this conception and have brought forward proof in support of my position. It is a pleasure to acknowledge here the material assistance that has been rendered me in this endeavor by the consistent results of my students. Realizing, however, the extensive character of the problem, I have confined the work to a somewhat limited field, but within this have made broad comparative studies. As the work progressed there was indicated the prevalence of a general plan of chromosome structure throughout the tracheate Arthropoda studied and it then became necessary to undertake careful researches within smaller groups, some of which have

<sup>1</sup> I am much indebted for assistance in carrying out work on Orthopteran germ cells to the Carnegie Institution, which made grant No. 16 for this purpose.

already been embodied in papers devoted to the Orthopteran families.

During the course of these investigations it became plain that there were variations from the type of maturation mitoses, and that these afforded facts which seemed to indicate that it might be possible to discover some correlation between individual chromosomes and body characters. It is the purpose of this paper to bring forward some of these facts and to suggest conclusions arising from our thus increased knowledge of the maturation chromosomes. In venturing these deductions I have had in mind their application to the particular forms studied, but at all times have tried to bring them into relation with facts derived from the study of other organisms. This, I believe, is justifiable in the present state of our knowledge, for it is done on the supposition that reproduction is, in the main, the same process throughout the range of organic forms. With the accumulation of observations the conviction is borne in upon us that the maturation mitoses of all organisms are, in general, of one pattern, and that the burden of proof lies upon him who would argue for individual types.

There is always the danger, to be sure, that we have not reached down to the basic facts, but are conceiving more superficial ones to be all important. This is, I imagine, unavoidable in the preliminary stages of an investigation, but it can lead to no harm if the facts in each case have been accurately determined. In the absence, therefore, of definite knowledge of the chromosomes in the germ cells of organisms exhibiting Mendelian characters or mutations we are warranted in supposing them to be of the same general character as the ones known until they are proved different.

The present paper is one of a series in which it is hoped to develop the history of the maturation chromosomes in the Orthoptera. Obviously this is a task of great magnitude and no far-reaching conclusions can be attained until a large series of forms has been studied. Already a not inconsiderable number has been worked over, and each year additions are made. Recently I have been devoting myself again to the family Acrididæ, and in some newly observed forms I have encountered certain peculiari-

ties of chromosome structure which seem to me of considerable importance. Some of these will here be considered.

It will hardly be necessary to enter into any account of the chromosomes in the Acridian family since this subject has already been discussed in a former paper ('00). Familiarity with the spermatogenesis of these Orthoptera will, therefore, be assumed and only such details gone over as are new or, at present, better understood.

The forms upon which the new observations were principally made are three species of the Acridiinaean genus *Hesperotettix*, and a species of *Mermiria*, a Tryxaline. While the facts stated have to do with these forms, they derive their importance from their relation to what appear to be common processes in the groups to which they belong. Much more work is, therefore, involved in the attainment of these results than would appear on first thought, and the basis for theories is correspondingly widened. In addition to the facts gained from the species mentioned, confirmatory evidence on a number of points afforded by some incomplete observations on *Chortophaga viridifasciata*, an Acridian, and *Anabrus*, a Locustid

## II. OBSERVATIONS.

### 1. *Number of Chromosomes in the Family Acrididæ.*

It may be recalled that in previous papers I have not laid much stress upon reported numbers of chromosomes, because of the difficulties involved in securing accurate enumerations. Nevertheless the full importance of this knowledge has not lacked appreciation, and latterly more attention has been directed toward the determination of the number of chromosomes in the different species of Acrididæ. In order to avoid the operation of the personal factor as much as possible, camera lucida drawings were made in considerable numbers from time to time and laid away. Finally the drawings were taken and the counts tabulated. As only the clearest cases were used for drawing, and as every precaution was taken to see that the entire complement of chromosomes for each cell was present, it is thought that the figures are reasonably accurate. Since this is the judgment of one who has at all times been decidedly critical toward the subject of chromosome enumerations, it may lend assurance to the results.

Regarding the enumerations I would say that much confidence is reposed in those of the spermatocyte elements, but that there is less certainty attending the figures derived from the spermatogonia. This is due to the fact that the latter cells are relatively small and the chromosomes very large, so that the elements are not well separated and clear. There is no fusion of the chromosomes in the metaphase, but they are long and sinuous and their limits hard to discern.

In general, then, it was found that for the family the number of chromosomes in the spermatogonia is 23 and in the first spermatocyte 12. Exceptions were found in *Hesperotettix* which has 23 in the spermatogonia and 11 in the first spermatocyte; and in *Mermiria* which has 23 in the spermatogonia and 10 in the first spermatocyte. Careful study revealed the fact that the exceptions are only apparent, and that the reason for the deviation from the family character is due to unusual associations of the spermatogonial chromosomes in the spermatocytes. This is brought about by the action of the accessory chromosome which here gives further evidence of its highly important character. It will be well to outline the history of the chromosomes in these genera separately and then refer to the principles of association involved later.

## 2. The Chromosomes of *Hesperotettix speciosus*.

It is not my intention to discuss the whole group of chromosomes in this species, but merely to give the history of the most strongly marked element. I hope subsequently to make a careful detailed study of the germ cells of the various species of this genus to establish the relations of the entire complement of chromosomes, but at present that is not possible.

If we examine the spermatogonial mitoses of this species we find that the chromosomes are of the usual rod-shape type, but among them there occurs one that is peculiar in being bivalent

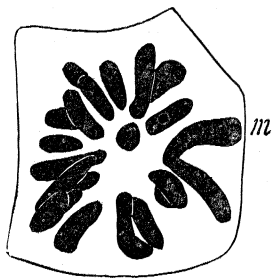


FIG. 1. Polar view of a spermatogonium of *Hesperotettix speciosus* (all the drawings of this genus were made from *speciosus* material) in metaphase, showing a tetrad "m." Not all the chromosomes are drawn.

instead of univalent. The chromatids composing this multiple chromosome<sup>1</sup> are amongst the largest in the cell and are easily distinguishable. During the anaphase it is seen that the multiple chromosome exhibits the so-called heterotypical form of division, and the figure produced is exactly the same as that resulting from the division of the tetrads in the first spermatocyte. In reality we have here a tetrad that is in every respect the same as those in the succeeding generation. A precocious synapsis of chromosomes in the spermatogonia is responsible for the unusual type of division in this generation of cells.



FIG. 2. The hexad multiple chromosome of *Hesperotettix* in the first spermatocyte prophase. The accessory chromosome "a.c." is homogeneous and the ordinary chromosomes granular, as is usually the case for these elements at this stage.

There can be no mistake about the nature of this multiple chromosome, for the line of fusion between the two chromosomes is clearly marked, and the mantle fibers of the metaphase attach at the center of the U-shaped element. In the anaphase the contrast between this chromosome and the others is very marked, for the daughter chromosomes of the latter ascend to the poles as straight rods with the fibers at the ends, while the former are U-shaped and have the fibers annectent at the center, or where the chromatids are joined together.

The early prophase of the first spermatocyte shows this bivalent element among the others, which have by this time also become bivalent, but it may still be distinguished by its greater length. When the chromosomes commence to shorten and condense the accessory chromosome attaches itself to one end of the large bivalent element, thus forming a trivalent chromosome. As thus constituted the multiple chromosome is much longer than any of the others, and clearly shows the limits of the three parts. A very peculiar condition prevails at this time. As is usually the case in the prophase, the ordinary chromosomes are granular and irregular in outline, while in striking contrast the accessory end of the multiple chromosome is homogeneous with sharply cut boundaries. The trivalent chromosome, or hexad, thus

<sup>1</sup> I shall use the term "multiple chromosome" for all elements containing more than two chromatids.

exhibits a very unusual appearance, because of the heterogeneous condition of its parts. Besides this structural difference, the accessory chromosome is further made noteworthy by the fact that it is shorter than the other thirds of the multiple element.

When the mitotic figure of the first spermatocyte is formed the hexad takes a position parallel to the axis of the spindle with the division between the parts of the original bivalent chromosome in the equatorial plate. As it lies thus it is almost as long as the spindle, but has approximately two thirds of its length on one side of the equatorial plate. This greater portion includes, of course, the accessory chromosome. Since the fibers always attach to the ends of the chromosomes, the accessory becomes bent away from the spindle and lies at a more or less obtuse angle to the rest of the chromosome. The mantle fiber then attaches to the angle thus established. A similar arrangement is mentioned by de Sinéty for the phasmid *Leptynia*.

With the beginning of the anaphase this multiple chromosome separates at the point where the two chromosomes were united in the spermatogonia, so that to each end of the spindle there goes one of the spermatogonial elements, but the accessory chromosome, on the contrary, becomes a member of only one of the daughter nuclei. Thus it happens that in the first spermatocyte where the quantitative division of the other chromosomes occurs this one element is divided qualitatively. In effect this is

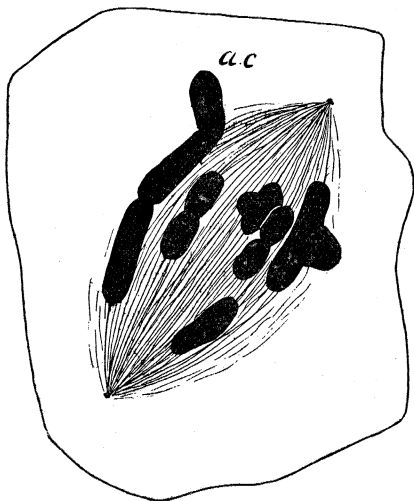


FIG. 3. Lateral view of the first spermatocyte prophase with a number of the chromosomes drawn. The hexad is shown in profile with the accessory chromosome, "a.c.," characteristically bent back at an angle. These, and all other drawings in this paper, were made under a camera lucida and are reproduced here at a magnification of 1,900 diameters.

also a qualitative division of the accessory chromosome which here exhibits the same behavior as has been described for the Locustids, the difference being that in the case of *Hesperotettix* there is a close association between the accessory and an ordinary tetrad. It would seem

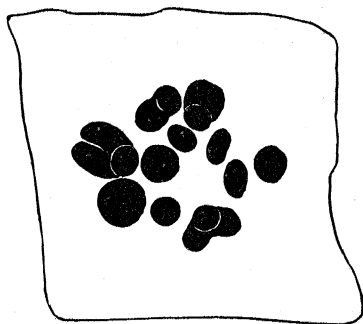


FIG. 4. Polar view of first spermatocyte metaphase, *Hesperotettix*, showing all the chromosomes of the complex.

that there is here an attempt on the part of the accessory chromosome to establish the usual relationships that are formed between chromosomes at this period of the maturation process. To this extent the element departs from what has been regarded as one of its most characteristic features, that of exclusiveness. As a matter of fact, however, all the

later work upon this structure has tended to show similarities to ordinary chromosomes rather than differences from them, and we are not surprised, therefore, to find it uniting itself with another

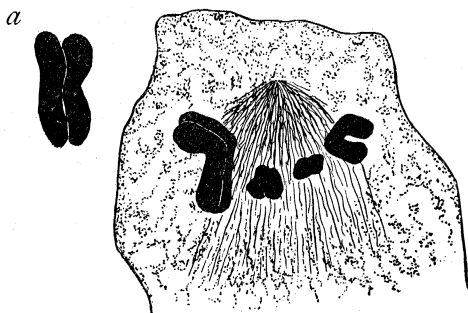


FIG. 5. Lateral view of one pole of first spermatocyte anaphase, *Hesperotettix*, with four chromatic elements drawn. The multiple chromosome at the left consists of the accessory chromosome and one half of the tetrad to which it was united. The relative positions are the same as in Fig. 3. Fig. 5a represents such a multiple chromosome *en face*.

chromosome in the ordinary manner. Being the odd member of the group it is unable to accomplish this step in the usual way and is therefore forced to become a member of a hexad element.



Why it should always be the same tetrad that is selected for this association is not clear, and will perhaps become apparent only when we learn the meaning that attaches to the intimate association among the maturation chromosomes.

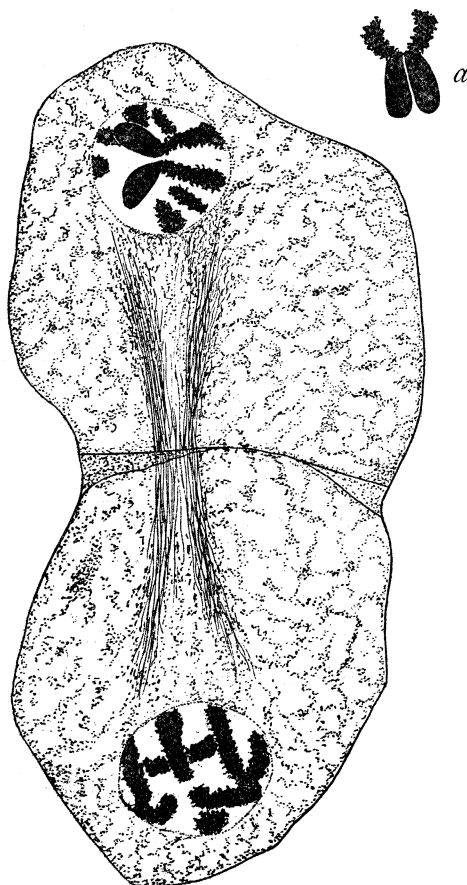


FIG. 6. Telophase of first spermatocyte of *Hesperotettix*. At the upper pole is the multiple chromosome in which the accessory chromosome remains homogeneous while the other element of the tetrad has again become granular. Homologous chromatids are well separated. Fig. 6a shows a similar chromosome with the accessory chromatids less divergent.

The close connection thus established by the accessory chromosome persists through the later periods of the maturation process. In the telophase the pair of chromosomes, consisting

of the accessory and the half of the tetrad, very much resembles the ordinary chromatin elements of the prophase, being, as it is, tetrad in character. Here as always, however, the accessory remains homogeneous while the associated chromosome becomes granular like its fellows. With the establishment of the second spermatocyte mitotic figure this oddly constituted tetrad takes its place in the equatorial plate with the mantle fiber attached at the point where the accessory chromosome is joined to the other one. Since the accessory is the shorter the fiber is not inserted at the middle of the chromatin rod but slightly to one side. The normal form and position of the chromosomes of the second spermatocyte in metaphase is that of a split rod pointing radially away from the axis of the spindle with the chromatids placed one above the other in the plane of the spindle axis. While all of the remaining chromosomes of *Hesperotettix* are thus arranged, the accessory chromosome and its mate are bent upon each other so as to present an angle to the spindle. It thus happens that in the anaphase there is apparent a heterotypical division of the multiple chromosome in which the resulting V-shaped loops each have one arm shorter than the other. It is now evident that the chromosome associated with the accessory has taken part in a heterotypical division in the spermatogonia and in the second spermatocyte, and in each case the plane of division corresponds to the original longitudinal cleft of the spireme thread. Because of the early association between the accessory and the tetrad there can be no doubt regarding the planes of division in the hexad.

I have not as yet attempted to work out in detail the specific characters of the *Hesperotettix* chromosomes, although I have that in mind for an early investigation. But even in the preliminary study here presented there have become apparent specific differences in the first spermatocytes which seem to be constant and which I will briefly notice. The description given above is based upon *Hesperotettix speciosus*, a form of larger size than the others and with strongly marked characters. Besides this there are in the same habitat two other species that are somewhat common and which are plainly different from *H. speciosus* but resemble each other in size and general appearance. This close resemblance caused my collectors to confuse the material from

which slides were made, and so I am not sure whether I have *H. pratensis* or *H. viridis*. I am tolerably sure that both are represented, although I have not as yet been able to detect differences enough in the cells to separate the preparations into two groups.

Despite the uncertainty regarding the exact character of the material, it is clear enough that it is not from *H. speciosus*, so that we know that any differences manifest in the cells will be between *speciosus*, definitely identified and described above, and either *viridis* or *pratensis*. From this comparison it is interesting to find

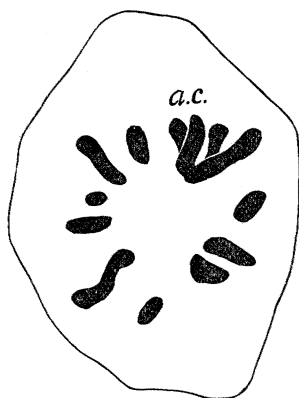


FIG. 7. A polar view of the second spermatocyte of *Hesperotettix* containing the accessory chromosome "a.c." It forms the smaller half of the tetrad. Not all the chromosomes present.



FIG. 8. Fragment of a second spermatocyte of *Hesperotettix* in metaphase showing the tetrad containing the accessory chromosome and two ordinary chromosomes.

that there are constant differences in the germ cells which are correlated with constant differences in body structures. So far I have made no attempt to trace variations beyond those shown by the hexad multiple chromosome. Even here only a start has been made, but it will suffice for my present purpose merely to show that there are differences between species of a genus in germ cell architecture.

First we must notice that there are present in both species multiple chromosomes of the same sort. This must be regarded as a generic character, and for specific differences it will be neces-

sary to look for modifications in size and proportions of parts. In drawings made at a magnification of 2,875 diameters it is found that the accessory chromosome of *H. speciosus* in metaphase measures on an average about 12 mm. while in *H. viridis* (?) it is near 11 mm.

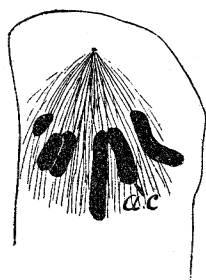


FIG. 9. A similar cell in anaphase. The disproportion between the accessory part of the dyad and the other member is well exhibited.

This difference is only slight, but if the chromosomes associated with the accessory are measured it will be found that the variation in size is considerable. Thus in *H. speciosus* the average length is in the neighborhood of 20 mm. while in *H. viridis* it is not over 15 mm. Here is a very pronounced specific variation which is probably accompanied by corresponding variations in the other chromosomes. Along with this difference in size of the chromosomes there goes a corresponding variation in the achromatic figure. The spindle in the first spermatocyte of *H. speciosus* is long and slender, while in *H. viridis* (?) it is short and heavy. There are probably many other less obvious differences

which I have not discovered in this preliminary survey. I hope in time to present these in detail.

### 3. *The Chromosomes of Mermiria sp.*

In the spermatogonia of *Mermiria* there is again found the heterotypical mitosis of chromosomes. The early synopsis of chromosomes, which is the occasion for the unusual form of mitosis, is encountered very frequently in spermatogonia, and I shall have occasion to refer later to instances in certain species where it is very marked. In the prophase of the first spermatocyte of *Mermiria*, there is again found a multiple chromosome which shows the same constitution as the one in *Hesperotettix*. The pronounced difference between the smooth homogeneous accessory chromosome and the rough granular elements of the tetrad joined to it is strikingly shown in the beautifully clear nuclei of this Tryxaline. So far the case is parallel to that exhibited by *Hesperotettix*, but just before the metaphase a singular and entirely unique association of the hexad multiple chromosome

of the prophase with one of the tetrads occurs. This is brought about by the end to end union of the parts which produces a pentivalent chromosome, or decad. So far as I know no such a chromosome as this has ever before been described.

The metaphase exhibits this strikingly peculiar chromosome extended along the length of the spindle parallel to its axis. The terminal parts are variously placed, sometimes being bent back parallel with the middle portion, sometimes extending out at right angles to it, and again being directed upward at an obtuse angle. Frequently the two terminal elements are differently inclined to the middle portion. In any event the archoplasmic fibers attach, not at the free ends of these chromosomes, but where their other ends join the

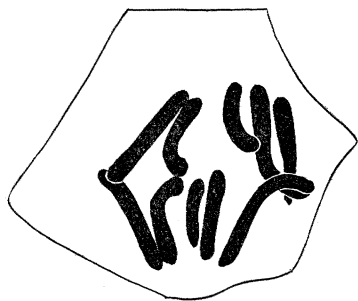


FIG. 10. Lateral view of some of the chromosomes in the metaphase of a spermatogonium of *Mermiria*. The multiple chromosome shows its tetrad character well.

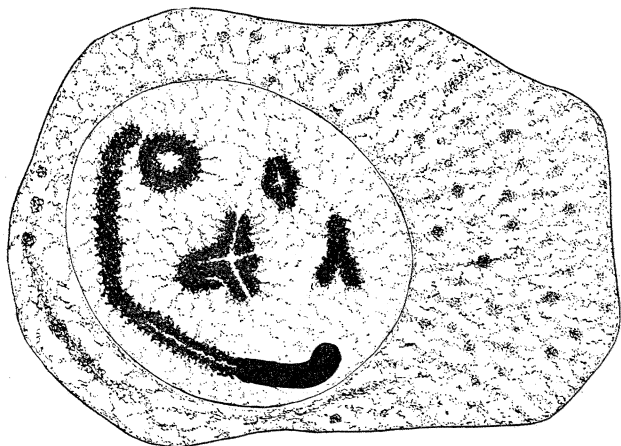


FIG. 11. Prophase of first spermatocyte of *Mermiria* showing particularly the accessory chromosome attached to a tetrad as in *Hesperotettix*. The organization of the cytoplasm is also indicated.

main shaft of the element. One point which I have not yet been able to determine with certainty is the position of the accessory

chromosome in the multiple element. Whether the tetrad that is added to the multiple chromosome attaches to the accessory end of the trivalent element of the prophase, or to the other extremity, I have not made out with certainty. The final result of the divisions would not be different in either case.

Upon the separation of the chromosomes in the metaphase the multiple chromosome is divided so that to one pole there goes a trivalent element and to the other a bivalent one, the difference in valence being due to the presence of the accessory chromosome in one daughter cell. There occurs here an entirely unique separation of chromosomes, for by means of it *entire*

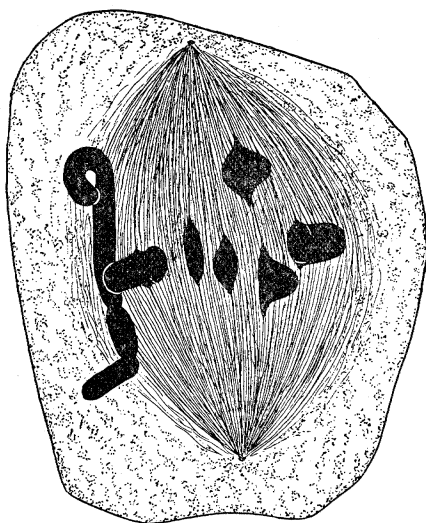


FIG. 12. Metaphase of first spermatocyte in *Mermiria* showing the decad in profile and a number of the tetrads. Observe that the fibers attach at the point of contact between two chromosomes and not at the free ends of the chromosomes. A very large part of the cytoplasm is organized into the spindle and the remainder of it is measurably polarized.

*tetrads pass into the second spermatocytes.* If these bivalent structures are always produced by the fusion of paternal and maternal chromosomes, then in this case both such pass into one cell. The alternative possibility that they are not homologous chromosomes will be discussed in the latter part of this paper.

When the second spermatocyte mitotic figure is formed it is seen that the accessory has separated from the dyad with which

it was united and has divided longitudinally as usual. But besides the accessory and the ordinary dyads of the second spermatocyte, there is present in each cell a tetrad which was a part of the multiple chromosome and which did not undergo division in the first spermatocyte. This may be found occupying on the second spermatocyte spindle such a position as tetrads usually occupy in the first spermatocyte, and under these circumstances it divides in the customary longitudinal manner. Here again there is a heterotypical mitosis along with the ordinary type, a condition which was also present in the spermatogonia. In both cases there is indisputable evidence that the plane of separation is along the original longitudinal split of the chromatin thread.

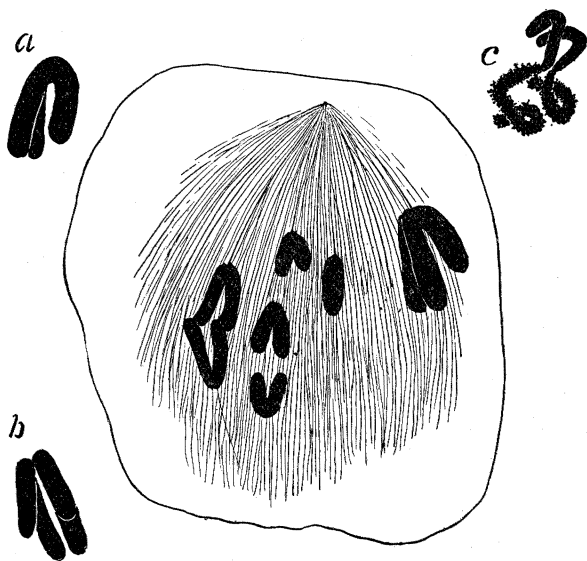


FIG. 13. Early anaphase of first spermatocyte in *Mermiria*. Only one pole of the spindle in the section and a few of the chromosomes. The method of the dyad separation shown in the tetrads. At the right of the spindle is represented a tetrad derived from the decad. Similar elements are shown in "a" and "b." At "c" is drawn the same structure in the telophase, where the homogeneous character of the accessory chromosome is in evidence.

A careful enough study of these cells has not yet been made to determine whether the pair of chromosomes in the second spermatocyte that remain united is the one which reappears in the spermatogonia of the next generation or not. It may not be

possible to ascertain this positively under any circumstances, but I believe that definite enough information could be secured by a comprehensive study. Considerable importance attaches to this as will be shown later.

In the Tryxalines the organization of all the cell contents is complete and precise at the time of the first spermatocyte mitosis. Practically the entire cell takes part in forming the bipolar mitotic figure. It is interesting to observe that the greater portion of

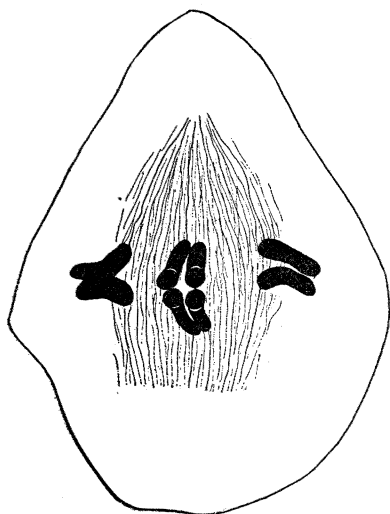


FIG. 14. Portion of a second spermatocyte of *Mermiria* in which the division of the tetrad coming from the decad of the first spermatocyte is shown along with that of the dyads.

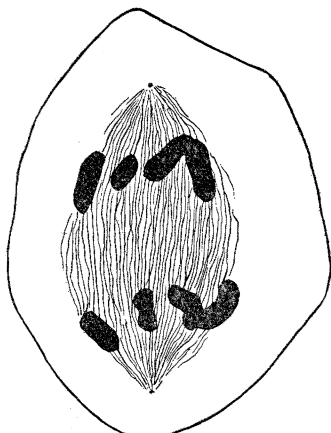


FIG. 15. Anaphase of the second spermatocyte of *Mermiria* showing the separated dyads of the tetrad and halves of ordinary dyads.

the cytoplasmic fibers lie outside of the circle of chromosomes that show in a polar view of the metaphase. At this time the chromosomes are scattered along in the spindle, forming no definite plate, and seem to divide independently and unaided.

This independent action of the chromosomes and the disproportion between them and the cytoplasmic figure would indicate apparently that the formation of the spindle is not to produce a mechanism for the separation of the chromosomes, but is rather for the purpose of securing an accurate division of the cell materials. This assumption is further supported by the observa-



tion that the same chromosomes that are involved in the first spermatocyte mitosis, where the spindle fills the entire cell, in the preceding generation, the spermatogonia, divide around a spindle that is so small as to be practically negligible as a motor apparatus for the movement of the chromatin. The spermatogonial spindle is indeed so diminutive as to be almost invisible among the relatively huge chromosomes that surround it, and so short as to be a fraction of the length of the chromosomes.

If the mitotic figure is purely, or even principally, a mechanical arrangement for the separation of the chromosome halves, then there would be some proportion between the spindles of successive generations which have to do with the same chromosomes. The ability of the chromosomes to execute independent movements is proven by the action of the accessory in wandering to one pole of the spindle in advance of the other elements, as well as by the long series of movements performed by them in the prophases.

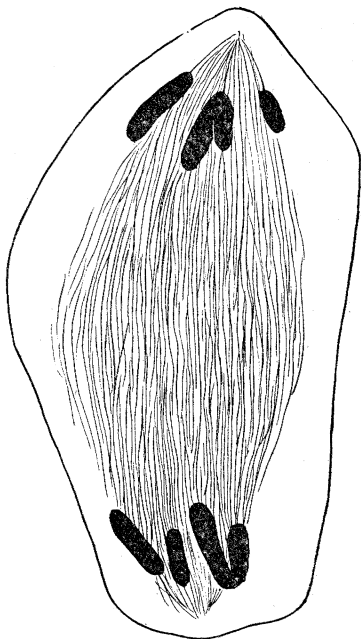


FIG. 16. Late anaphase of second spermatocyte of *Mermiria*. Here are represented later stages in the separation of such elements as are shown in the preceding figure.

#### 4. *Certain Chromosomes of Chortophaga viridifasciata.*

Besides the instances of unusual chromosome associations mentioned for *Hesperotettix* and *Mermiria* I am able to bring forward others which will serve to show that the conditions present in these forms are not pathological or abnormal. The most pronounced case of synapsis of spermatogonial chromosomes is exhibited by *Chortophaga*, an *Ædipodinae*. I observed and photographed cases of this three years ago, but did not attach much

importance to the condition until I recently encountered it in a number of other forms.

The spermatogonia of this genus show numerous pairs of chromosomes when viewed from the pole, in which the evidence of the end to end union of univalent chromosomes is unmistakable. The number of these pairs is not constant, but as many as four have been encountered in one cell. A side view of an

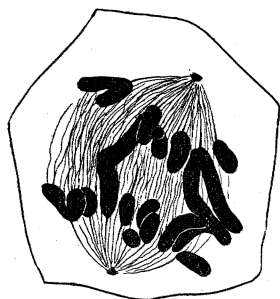


FIG. 17. Lateral view of a spermatogonium of *Chortophaga* in metaphase. The separation of multiple chromosomes along with simple ones is well shown. This is another good illustration of heterotypical divisions in the spermatogonia.

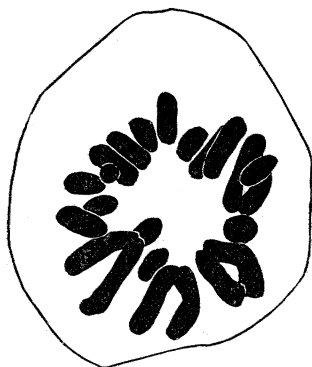


FIG. 18. A polar view of a similar cell in which appear four tetrads. This is an exceptionally good illustration of early synapsis of the chromosomes.

anaphase shows very clear heterotypical divisions among the chromosomes, the remainder of which are divided in the usual way. The subsequent history of these I have not worked out.

### 5. *Certain Chromosomes of Anabrus.*

During the course of my studies upon Locustid genera I was caused not a little difficulty by an oddly formed chromosome in the spermatocytes of the genus *Anabrus*. At the time I was obliged to confess myself beaten in the endeavor to determine the constitution of this element. That it had to do with the accessory chromosome I was thoroughly convinced, but that it was unusual in some way I was equally assured. Not until I had become familiar with the hexad multiple chromosome of *Hesperotettix* did the matter clear itself up. Having learned the pos-

sibility of an association of the accessory chromosome with one of the bivalent structures of the first spermatocyte I was soon able to see that the peculiar chromosome of *Anabrus* was another such a multiple chromosome as that of *Hesperotettix*. There is this difference between them, however, that in *Hesperotettix* the accessory chromosome is the small, univalent element, while in *Anabrus* it is proportionately very large, causing the tetrad with which it is associated to appear as an appendage at one end.

The multiple chromosome of *Anabrus* is a striking illustration of a fact to which I have often made reference, *i. e.*, to the relation existing between chromosomes and the attached archoplasmic fibers. *In all tetrad elements the fibers are annectent at*

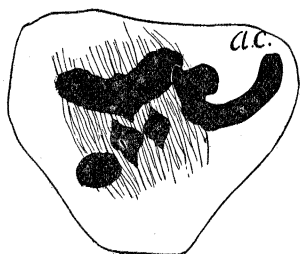


FIG. 19. Oblique view first spermatocyte of *Anabrus* in metaphase in which appears a multiple chromosome consisting of the accessory chromosome "a.c." and a small tetrad, several small tetrads and the one large one.

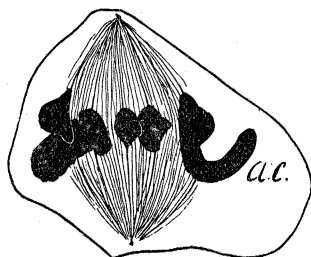


FIG. 20. Lateral view of first spermatocyte of *Anabrus* in metaphase exhibiting the same structures represented in the preceding figure. Note the attachment of the fibers to the hexad.

*the fused ends of the chromosomes, representing the plane of the future reduction division, and never at the free ends.* When the accessory is added to a tetrad in *Hesperotettix* the arrangement is disturbed somewhat in order to allow the insertion of one fiber to the point of contact between the accessory chromosome and one member of the tetrad, while the fiber to the other centrosome finds its connection at the free end of the tetrad.

Such a condition obtains also in *Anabrus* resulting in the production of a very singular appearing chromosome. Since the accessory is so very long it seems as if the fibers from both centrosomes attach near one end of the multiple chromosome, but as

a matter of fact one is connected where the accessory joins the tetrad and the other at the opposite end of the tetrad. From the variation in shape of the tetrad portion of the hexad it would appear possible that it has the accessory attached to the side and so divides longitudinally, but this I have not yet determined. Frequently it happens that the free extremity of the long accessory chromosome lies near the pole of the spindle, but in metakinesis it is the other end that moves toward the centrosome. In its

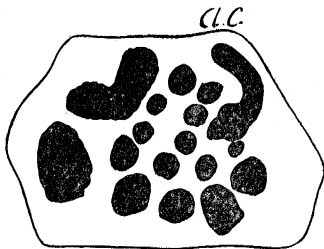


FIG. 21. Polar view of a similar cell with all the chromosomes drawn.

passage from the equatorial plate to the pole this end of the chromosome is bent upon the other moiety producing a U-shaped figure. I have not had opportunity to trace the later history of chromosomes thus associated, but have little doubt that they conduct themselves after the manner of similar ones in *Hesperotettix*.

It is thus shown that in three of the Orthopteran families, *i. e.* Acrididæ, Locustidæ, and Phasmidæ (de Sinéty) a hexad multiple chromosome is found in the first spermatocyte of certain species. Doubtless it exists in many others not yet studied and may reasonably be expected to occur in all the families of the order. In the presence of such elements we may also find an explanation of differences in number and behavior of chromosomes in related forms and in such as exhibit peculiar chromosomes not referable to the ordinary types.

#### SUMMARY OF OBSERVATIONS.

1. An Orthopteran family, the Acrididæ, is characterized by the possession of a definite and fixed number of chromosomes in its germ cells.
2. A genus of this family is marked by the arrangement of this series of chromosomes in a characteristic manner, which results in a precise sequence of divisions for these elements.
3. A species shows the grouping of chromosomes peculiar to the genus, but is distinguished by size differences of chromosomes, spindles and other cell parts.

4. The synapsis of chromosomes in pairs or other combinations does not occur in all species at the same time, nor do all the elements of the cell enter into these relations synchronously. There is accordingly no fixed synaptic phase.

5. Heterotypical divisions are observed in spermatogonia, first spermatocytes, and second spermatocytes, and in each case represent an ordinary longitudinal cleavage of the chromatin thread.

6. In cases of unusual associations of chromosomes the accessory is involved in the formation of the multiple chromosome.

7. Under all conditions the accessory chromosome goes to but one half of the spermatozoa.

8. When pentivalent multiple chromosomes are formed whole tetrads go into the second spermatocytes undivided.

10. In a single mitosis some of the chromosomes may divide qualitatively while the others divide quantitatively. This is due to unusual associations of the elements, and occurs regularly in the same way in all the cells of a generation.

11. Unless chromosomes are associated into multiple elements of higher valence than tetrads they divide longitudinally in the first spermatocyte and transversely in the second.

12. Tetrads divide longitudinally wherever found, either in spermatogonia, first spermatocytes or second spermatocytes. Multiple chromosomes of higher valence than tetrads divide transversely.

## CONCLUSIONS.

### 1. *Chromosomes and Somatic Characters.*

Two facts of first importance stand out as a result of these observations. The first is that a definite series of chromosomes accompanies the exhibition of a group of somatic characters that have been utilized by systematists for the inclusion of a number of genera into a family. The second fact is that these genera are characterized by a very precise architecture of their germ cells, whereby the series of chromosomes presents a definite arrangement and association which suffers modification in minor details in the different species of the genus. At the bottom of all, of course, lies the general fact that the chromosomes are morphological elements of the greatest constancy and importance.

Much has been done lately to show that the theory of the individuality of the chromosomes is well founded, but up to this time all that has been attempted has been to prove that in the species there is a constant series of chromosomes that appears in the successive generation of cells in each individual. I think that this has been done beyond reasonable question, in a number of forms and by different means. From the brief comparative study of the *Acrididæ* that I present here it now appears that not only are the chromosomes constant for the species, but also for the genus and family.

The far-reaching importance of this correlation between somatic characters and germ cell structure is at once apparent, for there is now some hope that it will be possible to establish the relations that exist between body characters and individual chromosomes. This has been the goal toward which I have been working ever since I observed the constancy in the behavior of the accessory chromosome and surmised its connection with the development of the male sexual characters—the first attempt, so far as I know to establish a relation between a particular chromosome and the same group of characters in different species.

The problem is unquestionably one of great complexity and difficulty, but I believe that with careful comparative studies of a great number of genera the rôle of the individual chromosome in development can be ascertained. If it is found possible, as I hope it may be, to apply experimental methods in breeding, etc., to these forms the results may be more quickly brought about. I have already made some tentative experiments, but have as yet accomplished nothing definite. Increased knowledge of the phenomena prevailing in these animals is bound to make the correlation between germ cell architecture and body characters more and more definite in details, and in connection with observations on other forms, will permit the formulation of some general principles that will be applicable to all organisms.

In the present state of our knowledge, however, we can do little more than erect a working hypothesis of a very general character, which doubtless will have to be modified with the apprehension of new groups of facts. It is to be borne in mind that our hypothesis must explain not only the appearance of the

characters in the individual and groups of individuals, but must also offer some explanation of the possible origin of new characters which serve as the basis for new genera and species — or, in other words, of variation. The most we can hope to accomplish by observation, in any event, is to determine the mechanism by which the germ cells operate to produce the body structures — the principle back of this can only be guessed at.

Before undertaking the formulation of any hypothesis it may be well to consider a few questions concerning the nature of body characters and their relation to each other and to the germ cells. The term "character" has a very broad and uncertain meaning. It may be applied to any structure of the organism from a vitally important organ to a trivial marking on the surface of the body. It is very much a question whether the characters belonging to these categories are equally firmly fixed upon the germ plasm, and for our present purpose it is desirable that we know whether there is any relation between the need of a character and its fixity in the chromosome. Again we should know the relations of the characters to each other in development. We shall have to ascertain, for instance, whether an organ or part develops purely as a result of the presence of one particular chromosome or whether the structure owes its initial stages to the action of one chromosome and its later development to the influence of another. It will be necessary to determine to what extent the chromosome acts as an individual and how far it functions as a mutually coöperating element in a complex. These considerations lead finally to the question as to the nature of the individual chromosome at different periods in the development of an organism. Is the chromosome of the just mature germ cell potentially the same as that of the tissue cell in the adult organism, or has the latter become progressively different throughout the ontogeny of the organism? If the second condition obtains then it is necessary to determine the means by which the chromosomes of the germ cells maintain their primitive nature through successive generations while the somatic cells in each acquire their various characteristics.

These considerations force themselves upon one as soon as the attempt is made to establish a relation of any sort between an

individual chromosome and certain characters of the body. Unfortunately we have no answers for these questions and they become, in fact, a part of the general problem.

As has been stated, the ultimate aim of these studies is to determine the relation between individual chromosomes and characters in the body, but this specific knowledge will come last of all and only after the most extensive investigations, so it is needless to say that as yet nothing has been discovered concerning the suspected relationship. What will first be accomplished will be the determination of the nature and behavior of the chromosomes in different species and from these observations some suggestions regarding the mechanism of the chromatin elements in heredity may be advanced. This knowledge may come about by a comparison of the germ cells and body characters in nearly related species, by observing the differences in germ cells of individuals that vary from the type of the species, or finally by experimentally disturbing the normal conditions in the germ cells and observing the effects upon the body. An attack on the problem must begin, then, by a search for differences between the germ cells of related species and between those of related genera, and in the present instance concerns certain forms that show very striking arrangements of the elements.

Upon the theory of the primary importance of the chromosomes in heredity we are forced to assume that the development of the characters in the individual of the genus *Hesperotettix* is the result of a definite composition and arrangement of the chromatic elements in the germ cells. Since definiteness of number, composition, and arrangement of the chromosomes always precedes the exhibition of a certain series of characters in the organism, it must be true that an alteration in either the number, composition, or arrangement of the chromosomes would be followed by the development of a somewhat different series of body characters. As I have previously mentioned, the number of chromosomes does not vary, nor is it possible to detect any difference in the composition of the chromosomes (although of course it occurs), but a characteristic arrangement of the chromosomes distinguishes this genus from others in the family, and so we must conclude that this is genetically connected with the subsequently appearing characters.



Within the well defined genus *Hesperotettix* occur the three clearly marked species, *pratensis*, *speciosus* and *viridis* and the germ cells of these exhibit the same grouping of chromosomes — at least of the ones most clearly distinguishable. Very probably when the complex is more thoroughly studied and understood there may be detected variations that are now obscure. Taking the case of the hexad multiple chromosome as being the clearest element to distinguish in the present state of our knowledge, it is found that in *viridis* (?) the tetrad portion shows a pronounced difference in size from that of the corresponding element in *speciosus*. Along with this are associated differences in the form and size of the spindle, etc. — a condition that may accompany, or be caused by, differences in the chromosomes. These peculiarities are connected with the exhibition of the body characters that are utilized for the purpose of classification. Whether these particular structural peculiarities are of the first importance or otherwise we have no way of determining, and this may delay the progress of our knowledge if there be differences in the power of transmission between characters of different rank in functional importance. We can not, therefore, with our present information, say, for example, that the variations of the structures mentioned are the cause of the difference in the size and proportion of the body in the two species, or whether they have to do with the surface markings on the exoskeleton. But when we know the full history of each chromosome in the complex and can follow its variations in all the species of the genus and can know how it differs from others in nearly related genera, then we may be able to associate a particular chromosome with a definite group of characters.

However, in these minutiae we shall have to await further and much broader knowledge, and for the present turn our attention to the more general questions that have centered around the larger cytological phenomena in their relation to body characters. It is not my intention to take up the question of the form and sequence of the maturation mitoses, since I intend to treat these matters *in extenso* in a later paper. It will suffice to say here that the enlarged views gained by more recent study have tended only to confirm me in the opinions that I have

previously expressed regarding these matters. Just now I wish to consider the bearing that the peculiar multiple chromosomes of *Hesperotettix*, *Mermiria*, *Chortophaga* and *Anabrus* have upon the general questions of heredity raised by the experimental work of the Mendelian school and by de Vries and his followers.

## 2. *The Chromosomes and Mendel's Laws.*

The first attempt to establish a correlation between cytological phenomena and the operation of Mendel's laws was made by Sutton in 1903, and was based upon Orthopteran material prepared and studied to a large extent in my laboratory. It was in thorough concordance with the laboratory results and represented the final step in the establishment of the theory of the individuality of the chromosomes and their relation to body characters. Done independently of Montgomery, it yet had as its fundamental idea the belief that half the chromosomes are paternal and half maternal, and that at the time of numerical reduction there is a union of homologous chromosomes in pairs. Montgomery clearly stated this idea of the union of parental chromosomes and should have due credit for it, but it is to Sutton's work that we are indebted for the detailed evidence of this fact, and for its theoretical application to the appearance of alternative characters in normal and hybrid breedings. It is this idea of definite association between chromosomes and characters and the explanation it offers for the purity of the germ cells and the recession of traits that renders the work of Sutton unique and makes it valuable.

There is no necessity for entering into any extended discussion of Sutton's results because, coming opportunely as they did with the renaissance of Mendel's conceptions, they immediately gained attention and are generally well understood. The essential feature of his conclusions is that there are in the somatic and immature germ cells a double series of chromosomes, one derived from the father and one from the mother. In synopsis this double series is united into one by the pairwise fusion of homologous chromosomes which remain in this state until the reduction division when they are separated again into a series which is of neither purely maternal nor paternal origin. This is offered as an explanation of the purity of the germ cells postulated by Mendel.

Sutton's views are formulated from careful comparison of size relations of chromosomes in the different generations of the male germ cells of *Brachystola* and represent the detailed proof of the conception expressed in more general terms by Montgomery.

Regarding the main view that the reduced number of chromosomes in the maturing germ cells is brought about by definite fusion of simple chromosomes into multiple ones of bivalent value, there now appears to be a pretty general agreement, and the older conception of a variety of processes has given way to the conviction that the same plan may be detected in all organisms when sufficiently studied. The final step in this direction is to regard this fusion of elements as a definite one between the same members in different generations of organisms. Such a correlation between germ cell architecture and somatic structure would be purely theoretical were it not for the fact that in the operation of Mendel's law there is an exact parallel between what is accomplished for the chromosomes in the maturation divisions and for particular characters in hybrid matings. While this is not an exact proof it raises the probability almost to a certainty and makes it practically impossible to doubt the accuracy of the hypothesis so far as it applies to purely Mendelian characters.

It is known, however, that many characters do not follow the course of those denominated Mendelian, and it now appears from the observations recorded in this paper that the simplicity of behavior by the chromosomes, assumed always to occur at the time of germ cell maturation, is not universal. The question naturally arises, then, whether the extremely simple explanation offered by Sutton is sufficiently inclusive.

Attention has already been called in previous papers to the probable importance of the prophase of the first spermatocyte in the matter of the hereditary transmission of characters. Upon the theory of the union of homologous chromosomes into pairs by synapsis<sup>1</sup> the nature of this becomes evident, for in the grass-

<sup>1</sup> By synapsis I mean the fusion of simple chromosomes into multiple ones, usually of bivalent value, according to the idea of Moore, who proposed the term. I would suggest that in order to avoid the lamentable confusion that has resulted from the misuse of this designation that a new descriptive word be applied to the condition of the nucleus in which the chromatin is found massed at one side of the vesicle, without regard to whether it is a normal phenomenon or not. To carry out this idea I shall call this stage the "*synizesis*" of the chromatin.

hopper this pairwise union of chromosomes continues in existence through fully half the life of the individual. If the chromosomes are centers of specific energies it is at this time that they would best be able to influence each other. Montgomery regards this as a phenomenon parallel to what occurs in the conjugation of the lower organisms, and so considers it a process of rejuvenation. This is a very loose term, and according to Montgomery's conception seems to mean nothing more than a stimulus to growth, for it is his conclusion that because of the conjugation of the chromosomes the germ cells immediately proceed to increase in size and attain dimensions in excess of those reached at any other period of their existence.

To me there is a much deeper meaning in this intimate and long continued association of the chromosomes which, as I have recorded for *Chortophaga*, may be established in the early spermatogonia. If there is to be a balancing of forces between homologous chromosomes this would seem to be the place where it must occur. We find, as a matter of fact, that in normal breedings there are produced germ cells that are either entirely pure in regard to certain characters or that develop intermediate results between the two extremes of the parents. The same individuals may show the alternative inheritance of one character and the blended inheritance of another. These phenomena would seem susceptible of a reasonable explanation if we should consider that in the first instance the interaction between the homologous chromosomes was slight, or entirely lacking, while in the second case it was more extensive. Upon the occurrence of the reducing division the linked chromosomes of the first example would separate practically unchanged, while in the other they would pass into the germ cells with different potentialities than they possessed before their synapsis.

If parents of different species were employed we might expect the same results and secure second generations of inbred hybrids that would show pure parental characters or various blends of these. Mosaics might easily be accounted for if we assume that the exchange between the chromosomes has been of such a character as to produce nearly a balance of the alternative characters. Through inequalities of division or by reason of different

environments, now one character would appear, now the other, and so produce the piebald result. Again we might conceive that the difference between two alternatives was so considerable and the disturbance of normal conditions so violent that the whole organization of the chromosomes would be upset with the result that a character distinct from that of either parent would be produced. These various alternatives are realized experimentally and I can see no simpler or more consistent explanation for them than the one I have presented.

### 3. *Multiple Chromosomes and the Chromosome Complex.*

As I have indicated already, there occur in *Hesperotettix* and *Mermiria* peculiar associations of chromosomes that are consistent from generation to generation of organisms. This can be no accident and undoubtedly has some fundamental meaning. It seems evident that the characters owe their orderly sequence in development to the organization of the germ cell elements and not alone to the mere presence of a particular chromosome. The experimental work of Boveri upon echinoderms and *Ascaris* would indicate the high importance of the individual chromosome, while the observations of Conklin upon the ascidian egg argues strongly for the view that what the chromosomes are able to accomplish in development depends largely upon the materials on which they have to operate—although we must not forget that these materials are probably produced by the action of chromosomes that came from the same original cell as do those of the germ cells.

It seems to me that these apparently somewhat contradictory observations speak unmistakably for the idea of precise organization in the germ cells and for mutual interaction between their parts. This thought comes home to me with particular emphasis after a study of the unusual precision in the arrangement of the cell parts of the spermatocytes of *Mermiria*. The evidence of the pentivalent multiple chromosome is of special importance for it shows that in order to maintain the identity of the chromatin complex from generation to generation there must be an accuracy not only in the division of the chromosomes in maturation but also in their coming together in fertilization. If it were not for

this definiteness of separation and recombination of the chromosomes then there would be all conceivable combinations instead of a definite and constant one such as is always found. An examination of the conditions in this genus cannot fail to put us in possession of some facts that could not well be obtained in any other way. It is necessary to go back to the early first spermatocyte prophase to secure an understanding of the structure of the chromosomes—a point that I have always insisted upon since the beginning of my work upon spermatogenesis. Here it is found that one of the tetrads has become united end to end with the accessory chromosome so that the planes of their longitudinal division are coincident. As is invariably the case in Orthopteran cells the accessory chromosome is univalent, so that there is thus produced a trivalent chromosome like that of *Hesperotettix*. Throughout the length of the chromosome there is a clear longitudinal split which, along the portion contributed by the accessory chromosome, is sharply marked because of the homogeneous character of its elements, while in the remainder of its length it appears somewhat interrupted on account of the granular structure of the tetrad region.

Some time near the dissolution of the nuclear membrane there is joined to this trivalent chromosome, by end to end union, one of the tetrads, thus producing a pentivalent element or decad. This element, we know, has a division running its length and corresponding to the longitudinal split of the chromatic thread, although in its homogeneous condition it is, like that of all the other chromosomes, obscured. In the metaphase of the first spermatocyte, as I have before stated, the separation of the chromosomes takes place in such a way that to one of the daughter cells there goes a tetrad and to the other a tetrad plus the accessory chromosome. For these elements the first maturation mitosis represents a reduction division and one of a very unusual character. At the same time, however, the other chromosomes are dividing longitudinally. Of this there can be no doubt for in the Tryxalines the ring chromosomes are numerous and in *Mermiria* as many as five or six may be found in one equatorial plate. This evidence is unmistakable to one who has a knowledge of their structure gained from a study of their formation in the

prophase, and their position in the equatorial plate, together with their relation to the mantle fibers in the metaphase and anaphase. I cannot stop here to enter into a criticism of the entirely erroneous interpretations of these rings by which de Sinéty proves a double longitudinal division and Montgomery a prereduction.

The probability of the occurrence of equational and reduction divisions in one mitosis is one against which I have previously argued strongly, because whenever reported the cases have lacked the support of thorough observation. The failure of the accessory chromosome to divide in the first spermatocyte mitosis, which is equivalent to a reduction, was the first authentic instance of this complexity, and now we have the case of the multiple chromosome in *Mermiria*, which furnishes further indisputable evidence of the two types of division in one mitosis. In the face of this evidence we must accept the fact and seek an explanation.

This is a matter of secondary importance compared with the question of the probable distribution of the chromosomes to the four spermatozoa arising from each first spermatocyte. It would appear at first glance that from the complexity introduced by the unusual arrangement and distribution of the chromosomes in *Mermiria* there must be a great many possibilities for variation in the chromosome complex, but if we accept the theory of the continuity of the chromosomes and remember that always the same complex appears in each first spermatocyte, then we must conclude that the mechanism of separation, distribution and recombination is a precise one. On the other hand, it is evident that the spermatozoa cannot all be alike, and we have to deal with different categories. This fact has been recognized for some time with regard to the accessory chromosome, but by the unusual combination of parts in the multiple chromosome (decad) of *Mermiria* there comes about an additional differentiation. The precise nature of this I have not been able yet to determine, on account of the absence of some prophase stages in my material. This hiatus I hope to remedy by the acquisition of a larger series of slides, but meanwhile we are sure of some facts and these are sufficient for the present discussion.

Since entire tetrads pass into the second spermatocyte there

are produced four sorts of spermatozoa with regard to the combinations of chromosomes, but two kinds with respect to the presence or absence of certain ones of a multiple. In order that always the same combination of chromosomes (so far as size is concerned, and this appears necessary to satisfy the observations) should appear in the spermatocytes, it would be necessary for eggs with the missing elements to be present and to be fertilized with the proper spermatozoa. The exact nature of this coördinate action cannot now be determined for we are lacking sufficient data, but that it must exist seems apparent from the observation that always the same sized complex reappears in each generation of first spermatocytes. From even our limited knowledge it seems evident that there is great precision and definiteness of organization necessary to bring about in successive generations of similar cells the same grouping of chromosomes. That the entire cell is involved in this organization is, I think, indicated by my observations on the spermatocytes of *Mermiria* where it appears that practically the whole of the cell material is bipolarized and thus accurately divided by mitosis.

The fact that there exists an orderly sequence of concerted movements on the part of the chromosomes suggests many interesting possibilities and offers opportunities for many speculations and theories, but it would seem wise to await the determination of more facts and a careful coöperative study of the species involved before venturing into speculation. Because of the importance attaching to these observations it has seemed desirable to make them known now in the hope that similar phenomena may be observed in other objects. Every additional fact of this sort largely increases the prospect of our attaining an understanding of the mechanism of the hereditary transmission of characters, and if it can be found that a peculiar association of chromosomes is always accompanied by a characteristic arrangement of the body parts then we may begin to see the relation between germ cell architecture and somatic structure.

Among the uncertainties in my mind concerning the behavior of the chromosomes in *Mermiria* is one relating to the nature of the association of the chromosomes into the multiple element of the first spermatocyte. The tetrads seem of the usual type, *i. e.*,



have simple chromosomes of equal size, but when the deced divides it would appear as though there were some heterogeneity present, for in the anaphase one limb of the loop is longer than the other (Fig. 13). This may be due to the formation of a multiple chromosome partly from the accessory chromosome; otherwise it means that the tetrad is not constituted of homologous simple chromosomes. Aside from this there seems to be nothing to contradict the view that the tetrads represent the union of homologous paternal and maternal elements.

#### 4. *Phylogeny of the Chromosomes.*

By the determination of the fact that for the family Acrididæ the number of chromosomes is a constant we gain a new viewpoint for the study of chromosome descent. So long as it was thought that nearly related species were characterized by the possession of different numbers of chromosomes it was impossible to regard the individual chromosomes as very constant structures. We have accordingly such theories as Paulmier's, later endorsed and elaborated by Montgomery, by which certain chromosomes smaller than the others and somewhat different in their behavior in the mitoses are regarded as disappearing from the species and carrying with them the loss of certain characters.

On *a priori* grounds such an occurrence would seem to be very improbable, for the difference between any two species is so slight that the loss of any number of the chromosomes would be entirely disproportionate to the effect. As a matter of fact the difference between two species or two genera consists not so much in the presence or absence of certain characters, but rather in the modification of those possessed in common. If therefore we have a constant relation between a certain group of chromosomes and a certain series of body characters we would expect differences between individuals to come about, not by the loss of chromosomes but by the modification of their structure or relations. It seems to me that the incomplete observations which I am presenting in this paper strongly indicate that this is what takes place.

The Acrididæ are a group of grasshoppers well marked off from the other Orthopteran families by the possession of a series of

characters that are remarkably constant. It is, in fact, sometimes difficult to establish characters of sufficient importance to differentiate subfamilies by their presence or absence. This precision and fixity of bodily organization is accompanied by a corresponding stability of the chromosome complex, which indicates that throughout the family there is a correspondence between individual chromosomes and their products in development. By this I mean that if we can fix upon any particular chromosome by some peculiarity of structure or behavior and associate it with definite body characters we will find that same chromosome in all the species of the family governing the development of the same somatic structures. Individual chromosomes have therefore a continuity of descent in the same way that cells and organisms have.

Comparing the Acrididæ with the Locustidæ it appears that in the spermatogonia there is a difference of ten chromosomes in favor of the latter group. While these two families are well separated it is due more to differences of common characters than to the absence in one of characters possessed by the other. We must conclude, therefore, that the chromatin governing the development of these common characters is present in both families. It is evident, however, from the enumeration of the chromosomes, that it is differently associated in the two groups with the exception of that contained in the accessory chromosome. We cannot for this reason compare chromosomes with chromosomes throughout the whole complex of the two families and it is plain that the differences in structure are due to the differences in composition and association of the chromosomes. This is foreshadowed, or indicated, by the differences of association that prevail between genera, as is suggested by the appearance of multiple chromosomes. These associations may further point the way to an understanding of the differences in number between different families, the smaller one being brought about by the permanent union of independent chromosomes, rather than by the entire loss of elements.

##### 5. *Chromosomes in Variation.*

A discussion of the relation of chromosomes to one another in different groups leads to an enquiry into the relation of characters

to each other in various individuals. As is well known, between parent and offspring there may be a difference of characters such that if a sufficient series of pairs is taken there may be found an almost continuous seriation. Such variation is appropriately called "continuous." On the other hand it occasionally happens that between parent and offspring there occurs a sudden and sharp rearrangement of body characters, which remains constant. As opposed to the continuous variation this is called "discontinuous." Biologists are more and more inclined to place the origin of variation between parent and offspring in the germ cells and more specifically in the chromatin. Since, however, the types of variation are sharp and distinct there must be corresponding differences in the chromatin. We know so little about the relation this nuclear material bears to the development of characters that it is somewhat hazardous to venture an explanation of the mechanism involved. It seems to me, notwithstanding this, that we may gain some slight insight into the processes by a comparison of the chromosome groups.

Thus in the genus *Hesperotettix* the chromosome complex seems to be a fixed one, and in the different species there occur peculiarities that are constant. We are therefore warranted in assuming that if this uniformity were disturbed it would result in the development of a different series of characters. If, for instance, the hexad of the first spermatocyte in *Hesperotettix* should, for some reason, not be formed at the usual time of the coming together of the tetrad and the accessory chromosome, thus producing a different distribution of the chromosomes into the four spermatocytes, I think we may fairly assume that these cells would not cause the development of the group of characters which we associate with the genus *Hesperotettix*. In such an event we would have a mutation. This, of course, does not explain *why* the mutation occurs, but it accounts for the means by which the result is accomplished. There is in force here, possibly, the same principle that paleontologists have observed to be in operation in groups of animals that are in course of extinction. Here it is noticed that strange and unusual forms appear, and the closing history of the group is marked by the breaking up of the heretofore constant type into numerous and

heterogeneous subtypes. We do not know certainly that this is an occurrence of exactly the same nature as the present day observed mutation, but it is of the same character and is an evidence that stability of the germ plasm is disturbed by irreversible changes which, as I have pointed out, may find expression in different arrangements of the chromosomes.

Opposed to the sudden and pronounced changes in character combinations that mark instances of discontinuous variation stand the common examples of continuous variation, where there is present a graded series of inconstant and fluctuating variations. To my mind the two types of variation suggest different mechanisms of transmission. Discontinuous variation speaks of pronounced and irreversible alterations of the chromosome complex; continuous variation, on the contrary, suggests the idea of small changes in individual chromosomes, due to the impossibility of mechanically producing two exactly equivalent daughter cells. These latter variations are minute and of every conceivable character, but are inconstant and indeterminate. As a basis for the occurrence of these fluctuating changes we have the observed fact of the lack of exact correspondence in the size of chromosomes and other cell parts in the various cells of an organism, and the probability of a difference in the interaction of the chromosomes in synapsis. I can not refrain from again calling attention to the strong evidence that identical twins offer in support of the theory that the characters are fixed by the composition of the germ cells. Since these twins are the product of a single egg it is evident that they must have exactly the same chromosome complex, which, in development, will bring about a very close parallel in the characters produced under their control. No other pair of germ cells from the same two parents will ever produce two individuals that bear the resemblance to each other that identical twins do, because, by the laws of chance, it is improbable that any two pass through synapsis and the maturation mitoses and emerge from them with their chromosomes constituted in exactly the same way. Ordinary twins, coming from different eggs, are no more alike than children of successive births although they are developed under practically identical conditions, thus removing the possibility of environ-

mental differences. Therefore it appears that the fluctuating variations which occur in a series of organisms comprising a species are the results of minor differences in the chromosomes of the germ cells, due to the impossibility of exactly duplicating the conditions of union and separation of the paternal and maternal chromosomes in maturation.

Mutations on the other hand follow some unusual disturbances in the relations of chromosomes to each other, brought about by some change in the germ plasm whose cause we cannot now determine. So much, I believe, we may conclude from our present knowledge of the germ cells and their behavior in maturation and fertilization. As our detailed knowledge of the chromosomes increases we may be enabled to speak more definitely and certainly, but further information we must have and it is earnestly to be hoped that the chromosome groups of many species of these Orthoptera may be carefully and exhaustively studied in connection with observations upon body variation so that correlation between the two may be established.

ZOOLOGICAL LABORATORY, UNIVERSITY OF KANSAS,  
June 21, 1905.

#### NEW TERMS EMPLOYED.

##### *Definitions and Classifications of Chromosomes.*

Chromosomes are chromatin elements acting as unit structures during mitosis.

Chromosomes are of two general classes.

1. Simple — containing two chromatids in metaphase.
2. Multiple — containing more than two chromatids in metaphase and formed by the union of simple chromosomes.
  - (a) Tetrads, containing four chromatids.
  - (b) Hexads, containing six chromatids.
  - (c) Octads, containing eight chromatids (not yet observed).
  - (d) Decads, containing ten chromatids.

A chromatid is a half of a simple chromosome.

“Synzesis” — the unilateral or central contraction of the chromatin in the nucleus during the prophase of the first spermatocyte. A term proposed to avoid the misuse of the word “synapsis.”

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